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Relationships of the Saurischian Dinosaurs

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INTRODUCTION

The word "Dinosauria" was coined by Sir Richard Owen in 1842 as a designation for various genera and species of extinct reptiles, the fossil bones of which were then being discovered and described in Europe. For many years this term persisted as the name for one order of reptiles and thus became well intrenched within the literature of paleontology. Indeed, since this name was associated with fossil remains that are frequently of large dimensions and spectacular shape and therefore of considerable interest to the general public, it in time became Anglicized, to take its proper place as a common noun in the English language. Almost everybody in the world is today more or less familiar with dinosaurs.

As long ago as 1888, H. G. Seeley recognized the fact that the dinosaurs are not contained within a single reptilian order, but rather are quite clearly members of two distinct orders, each of which can be defined on the basis of many osteological characters. The structure of the pelvis is particularly useful in the separation of the two dinosaurian orders, and consequently Seeley named these two major taxonomic categories the Saurischia and the Ornithischia. This astute observation by Seeley was not readily accepted, so that for many years following the publication of his original paper proposing the basic dichotomy of the dinosaurs the

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name "Dinosauria" continued as a formal taxonomic term. It was perhaps owing chiefly to the work of von Huene that the two dinosaurian orders finally became generally accepted, for in 1914 he published at least two papers in which he stressed the reality of the orders Saurischia and Ornithischia, and he continued to insist upon this point in many subsequent works. Today the two orders of dinosaurs are universally recognized.

In 1878, O. C. Marsh proposed the name "Sauropoda" as a suborder of the Dinosauria, in one of a series of studies concerned with the Jurassic dinosaurs from Como Bluff, Wyoming, which at that time were being collected by Marsh's assistants in such prodigious quantities. "A well marked group of gigantic dinosaurs [which] differ so widely from typical Dinosauria, that they belong rather in a suborder, which may be called *Sauropoda*, from the general character of the feet" (Marsh, 1878, p. 412). Subsequently, in 1881, he presented an outline classification of the dinosaurs in which he used the name "Theropoda" as the designation for still another dinosaurian suborder: "Suborder Theropoda (Beast foot). Carnivorous" (Marsh, 1881, p. 423).

For many years the theropods and sauropods were considered as two among several suborders of Dinosauria, but, with the eventual acceptance of a division of the dinosaurs into two separate orders, it was quite apparent that these two particular suborders should be included within the Saurischia. Consequently during about the past half century the saurischian dinosaurs have commonly been subdivided into these two suborders, the Theropoda and the Sauropoda, a major taxonomic dichotomy that has gained wide acceptance.

The sauropod dinosaurs form a rather homogeneous group, and such subdivision as has been made of the suborder has been at the family level. Therefore they offer no great problem in classification. The case of the theropods is, however, different, because these dinosaurs show considerable variety in their adaptations and hence in their morphological structure. Consequently they have been classified within a number of families, which in turn have been variously grouped into larger taxonomic divisions of infraordinal or suprafamilial rank. To this particular facet of saurischian classification the remainder of the present paper is largely directed.

In 1941, von Huene (1914a) proposed two large subdivisions (*Unterordnungen* or suborders) of the saurischian dinosaurs, namely, the Coelurosauria and the Pachypodosauria. The first of these two suborders was to be composed of the small, hollow-boned, carnivorous dinosaurs; the second, of the large, heavy carnivores and of the sauropods. It will be

seen that von Huene in this classification abandoned the concept of the theropods as originally proposed by Marsh, while he relegated the sauropods to less than subordinal status, although he did not suggest that they should be diminished to family rank. This arrangement of the saurischian dinosaurs is unnatural in that it removes some of the larger theropods from a position contiguous to their small relatives, to associate them with the sauropods. It does, on the other hand, recognize the fact that the theropods are not a completely homogeneous group, as is shown below.

Von Huene in 1928 further formalized and modified somewhat the arrangement mentioned above by recognizing two major taxonomic divisions for certain saurischian dinosaurs. One of these was the Prosauropoda, for the reception of those heavily built Triassic dinosaurs, hitherto placed by many authors among the theropods, that obviously were more or less ancestral to the Jurassic and Cretaceous sauropods, and the other was the Carnosauria, to include the large, heavy, carnivorous saurischians. The Prosauropoda were included by von Huene with the Sauropoda within a larger category, the Sauropodomorpha, which with the Carnosauria formed the Pachypodosauria. Perhaps von Huene's views concerning saurischian relationships, which grew and went through various metamorphoses during the years, are finally expressed in the classification in his comprehensive book "Paläontologie und Phylogenie der niederen Tetrapoden" (1956). The larger subdivisions of the saurischian dinosaurs were there treated as follows:

"Ordnung Saurischia
  Unterordnung Coelurosauria
  Unterordnung Pachypodosauria
    Familien-Hauptkreis Carnosauria
    Familien-Hauptkreis Prosauropoda
    Familien-Hauptkreis Sauropoda"

This formal arrangement of the Saurischia stems not only from the earlier papers by von Huene, which are above cited, but also from certain other papers, particularly one published in 1928, one in 1954, and one, his monumental monograph on the saurischians, in 1932. In all his later work von Huene emphasized four points, namely, that the oldest saurischians are the coelurosaurs, that at an early date and from an ancestry common to that of the coelurosaurs the pachypodosaurs arose, that during Triassic times the pachypodosaurs were very similar, and that in later Mesozoic history there was in these latter a divergence, whereby the carnosaurs and the sauropods evolved along their separate lines of adaptation.

Von Huene's original, and in many ways penetrating, view of sauris-

chian relationships is somewhat at variance with what might be called the more conservative viewpoint, as expressed by various authors in earlier years. As mentioned above, Marsh created two dinosaurian suborders, the Theropoda and the Sauropoda, these being part of a series of suborders into which the early order Dinosauria, as then understood, was subdivided. In Woodward's classification of 1898, three suborders of Dinosauria were recognized, the one in addition to the Theropoda and Sauropoda being the Ornithopoda, to include all the ornithischian or "predentate" dinosaurs. In this arrangement Woodward followed Marsh, who in 1896 likewise presented a threefold subdivision of the dinosaurs. As mentioned, with the acceptance of the two separate dinosaurian orders, the Theropoda and Sauropoda naturally fell within the Saurischia.

Of course such an arrangement cuts across von Huene's Pachypodosauria, just as his Pachypodosauria cuts across Marsh's Theropoda. Whether or not these views can be reconciled is discussed below. If the suborder Theropoda is retained, the question immediately arises as to where to place the Carnosauria and the Prosauropoda. It is general practice to include both of these infraorders together with the Coelurosauria in the Theropoda, an arrangement that was presented by Romer in his classification of 1956, thus:

Order Saurischia
  Suborder Theropoda
    Infraorder Coelurosauria
    Infraorder Carnosauria
    Infraorder Prosauropoda
  Suborder Sauropoda

The two systems of splitting the Saurischia subordinally that are outlined, the one in which the order is subdivided into Coelurosauria and Pachypodosauria, the other in which it is subdivided into Theropoda and Sauropoda, confront us with a dilemma. There seem to be good arguments for both systems, and, if so, how can they be compromised? Are they mutually exclusive? Certainly if one separates the primary bipedal saurischians from the secondary quadrupedal forms, the subclasses Theropoda and Sauropoda seem to be a natural consequence. On the other hand, if one recognizes the obviously close relationships of the large Triassic carnivorous saurischians with those forms that are obviously trending toward the sauropods, there are good arguments in favor of a subordinal dichotomy, the branches of which may be labeled as Coelurosauria and Pachypodosauria. Perhaps, however, neither of these two apparently opposed systems of classification gives us a true concept of saurischian relationships. A re-examination of the evidence is called for.

THE PELVIS IN THE TRIASSIC SAURISCHIANS

In this respect the evidence of the pelvis is especially pertinent. The primary separation of the dinosaurs into two distinct orders has been based, first of all, on the structure of the pelvis. Since the two dinosaurian orders are undoubtedly valid taxonomic units, there are naturally various contrasting morphological characters that may be correlated with pelvic structure. Thus the skull in the saurischians is comparatively deep, with large temporal openings and preorbital fenestrae, the teeth are simple in structure, the fourth trochanter of the femur is never pendent, and so on, while in the ornithischians the skull may be very broad in comparison with its height, its fenestrae are frequently reduced or obliterated in various ways, the teeth are frequently complex in structure, the fourth trochanter of the femur is pendent, and again so on. There is no need to labor the point at this place.

Because the pelvis is so crucial a character in the delineation of the two orders of dinosaurs, perhaps it offers additional evidence as to subordinal relationships. Briefly, how does an analysis of pelvic structure accord with the grouping of genera that can be made within the Saurischia? But before this question is considered, let us look at the pelvis in the putative ancestors of the Saurischia, namely, the pseudosuchian thecodonts.

It is generally supposed that the origins of the Saurischia are to be found within the Ornithosuchidae or Erpetosuchidae, among the Pseudosuchia.[1] Certainly these comparatively unspecialized thecodonts, whatever may be their proper family name, which in their structure show various features that are characteristic of the saurischians, would seem to be the most reasonable group in reptilian phylogeny from which to derive the dinosaurs that are now under consideration. Unfortunately the erpetosuchids are not so well known as is desirable. Only a few genera constitute this family of reptiles, for the most part based on incomplete materials. Consequently our knowledge of what might be regarded as a typical erpetosuchid is composite, put together from various sources; nonetheless it is possible to get a reasonably valid idea of what these reptiles are like. They are comparatively small, lightly built, bipedal reptiles, with hollow bones, deep, open skulls, thecodont teeth, small forelimbs and long, bird-like hind limbs, and with a limited covering of dermal

[1] The taxonomic relationships of those pseudosuchians commonly placed in the Ornithosuchidae require re-examination and clarification. No such task is attempted here; the problem is now receiving the attention of A. D. Walker of Newcastle. The name "Erpetosuchidae" is used in the present paper as a designation of those pseudosuchians commonly classified as Ornithosuchidae (see Romer, 1956).

scutes on the back. The pelvis is characterized by two sacral vertebrae, a long, rather plate-like pubis, and a moderately elongated, constricted ischium. The acetabulum is closed. One cannot make unequivocal statements concerning the form of the ilium. In *Erpetosuchus*, *Saltoposuchus*, and *Hesperosuchus*, which may be considered representatives of these generalized pseudosuchians, this bone is missing from presently known materials. A good ilium is preserved in *Ornithosuchus*, but this genus may not be a pseudosuchian at all. Other so-called erpetosuchid genera either lack postcranial bones, as in the case of *Cerritosaurus*, or may be very doubtfully placed within this pseudosuchian category, as in the case of the several genera described by von Huene from Brazil. It is probable, however, that the ilium in the erpetosuchids was rather deep, with a moderate posterior elongation of the iliac crest.

Generally speaking, the pelvis that is here described could very readily have been derived from the pelvis of the South African Lower Triassic pseudosuchian *Euparkeria*, by elongation of the pubis and by some thinning of the ischium. Such a pelvis may in turn have given rise to the type of pelvis characteristic of some of the first saurischians, by further elongation and narrowing and a forward rotation of the pubis, by still further thinning of the ischium, by perforation of the acetabulum, by incorporation of a caudal vertebra into the sacrum, and perhaps by some minor changes in the ilium. The saurischian pelvis thus so briefly described is well exemplified in various Upper Triassic genera, such as *Palaeosaurus* or *Thecodontosaurus*.

To enlarge on the above characterization, one could describe such a saurischian pelvis as having a comparatively short and deep ilium, the lateral surface of which is mostly behind (and of course above) the middle part of the acetabulum. This ilium has a small and usually a rather sharp anterior point as the forward termination of the iliac crest, and this point invariably fails to extend as far forward as the pubic process of the ilium. There are three sacral vertebrae. The pubic process, or peduncle, is quite large and is widely separated from the ischial peduncle. In other words, the acetabulum is very large. From this description and from figure 1, the ilium in *Palaeosaurus*, for example, may be seen to be essentially a pseudosuchian ilium with the acetabulum hollowed out, forming a large open arch rather than a solid plate.

This type of saurischian ilium articulates with a very long pubis and a long ischium, these two bones forming an approximate right angle with each other, as seen from the side. The pubis is broad and meets its fellow in a long symphysis, so that the two pubes form an elongated, plate-like structure. Distally the pubis may be slightly expanded, while proximally

it is perforated by a thyroid fenestra, this latter feature occupying an expansion of the pubis which extends posteriorly beneath the acetabulum to about its middle point. Thus the pubis is in a sense a "twisted" bone, being formed of an upper, small, posteriorly directed plate which forms a part of the acetabular border, and of a lower and very large transverse plate which forms the bulk of the bone.

The ischium is a constricted and perhaps a rather rod-like bone, expanded at its upper end into a plate that makes in a general way a counterpart of the proximal portion of the pubis. This upper portion of

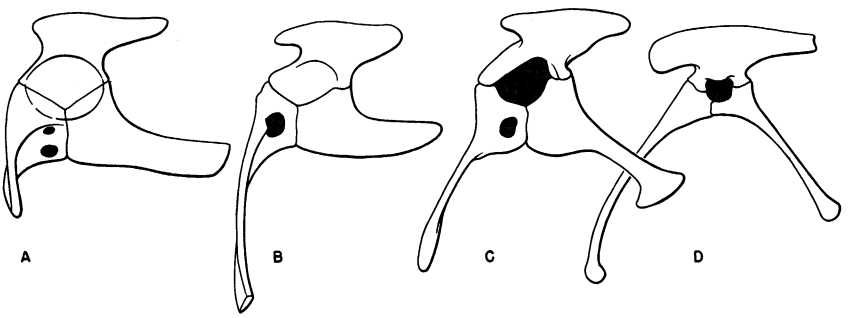

FIG. 1. A comparison of the pelves, as seen laterally from the left side. A. *Euparkeria*, a pseudosuchian. B. *Saltoposuchus*, a pseudosuchian. C. *Palaeosaurus*, a palaeosaurian saurischian. D. *Coelophysis*, a coelurosaurian saurischian. A after Broom; B and C modified from von Huene. Not to scale.

the ischium constitutes the posteroventral border of the acetabulum. The ischium is somewhat expanded at its distal end.

Here again, as in the case of the ilium, one may derive the pubis and ischium from the pseudosuchian condition. Such a derivation would involve some reduction in the proximal portions of the two bones. Various pseudosuchians have a long, "twisted," plate-like pubis with a thyroid fenestra, very close indeed to the saurischian pubis just described. The resemblance of the ischium in these pseudosuchians to that in primitive saurischians is not quite so close, but even here the step from the one to the other is comparatively small.

Contemporaneous with the late Triassic saurischian dinosaurs that are characterized by the type of pelvic structure just described are other saurischians in which the structure of the pelvis is markedly different. These are the saurischians generally designated, at least in part, as the coelurosaurs, the early members of a long-persistent dinosaurian group that carried on from the late Triassic to the end of Cretaceous time. The

coelurosaurs are best exemplified in Upper Triassic sediments by genera belonging to the family Podokesauridae, and of these genera *Coelophysis* is by far the most completely documented form.

Whereas the pelvis in *Palaeosaurus* and related dinosaurs may be very readily derived from the pelvis in certain pseudosuchian thecodonts, that of *Coelophysis* and its relatives shows striking departures from what may be considered as the primitive saurischian structural form. In *Coelophysis* the crest of the ilium is greatly elongated, so that this bone is relatively shallow as compared with its length, a decided contrast to the ilium in *Palaeosaurus* or *Thecodontosaurus*. Articulating with this long ilium are five sacral vertebrae (four in some genera). Anteriorly the ilium is no longer a small and rather sharp point, as in the ilium described above, but rather this part of the bone takes the form of an expanded plate, the front border of which is rounded. It projects far forward beyond the front of the acetabulum. Posteriorly the ilium projects even farther than it does anteriorly. Consequently the length of the bone is about three times its height, as contrasted with the ilium in *Palaeosaurus*, which is less than twice its height, or that in *Thecodontosaurus*, the length of which barely exceeds its height. Furthermore the ilium in *Coelophysis* and related genera is characterized by the subequal and short peduncles for articulation with the pubis and ischium, which may be contrasted with the large and rather long pubic peduncle in *Palaeosaurus* and its relatives. Thus the upper acetabular border in *Coelophysis* forms a nicely rounded arch, this in turn merging into the lower acetabular border, so that the acetabulum is in essence almost a perfect circle. In *Palaeosaurus* and other saurischians of its type the acetabulum is somewhat elliptical, or at least "skewed," owing in part to the difference in length of the two peduncles of the ilium. Finally, the acetabulum is relatively smaller in *Coelophysis* than it is in the dinosaurs that are here used for comparison.

The differences in the pelvis between *Coelophysis* and Triassic dinosaurs of the *Palaeosaurus* or *Thecodontosaurus* type extend to the two other bones of the girdle as well. Thus the pubis in *Coelophysis* is very long and constricted. Its proximal end is relatively narrow and is not "twisted" with relation to the pubic shaft. There is no thyroid foramen. Distally the pubis terminates in a small knob. Throughout most of their length the two pubes meet in a long symphysis, and taken together they form a comparatively narrow and elongated plate, divided at each end—at the proximal end into the two rami that articulate with the right and left ilia and ischia, at the distal end into two short processes, each ending in a knob.

The ischium in *Coelophysis* is likewise comparatively long and slender,

although not so long as the pubis. This bone is truly rod-like, having a facet for articulation with the ilium and a process extending forward to meet a similar process from the pubis, these two processes forming the lower border of the acetabulum. The end of the ischium is slightly expanded. The two ischia meet distally for about half of their length in a symphysis.

From these descriptions it is evident that two basic types of pelves are to be seen among the saurischian dinosaurs of Triassic age. One of these,

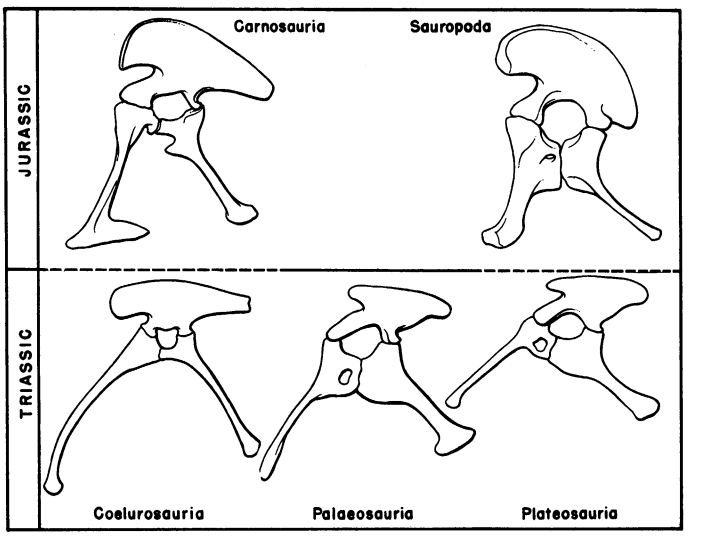

FIG. 2. Pelves of saurischian dinosaurs, as seen in left lateral view. In the Palaeosauria and Plateosauria the pelvis is of brachyiliac type, and from this form of pelvis the sauropod pelvis was derived. In the Coelurosauria the pelvis is of dolichoiliac type, and from this form of pelvis the true carnosaurian pelvis was derived. Modified from von Huene, Gilmore, and Osborn and Mook. Not to scale.

exemplified by the pelvis of *Palaeosaurus* and *Thecodontosaurus* and which is here designated as the "brachyiliac" type, is of relatively primitive aspect and may be derived quite readily from the pseudosuchian pelvis. The other, in the present paper called the "dolichoiliac" type, is certainly more advanced in form, but probably arose at a very early stage in saurischian evolutionary history from the brachyiliac pelvis. The brachyiliac pelvis as such did not survive beyond the Triassic period, but in a sense it continued in modified form as the pelvis of the Jurassic and Cretaceous sauropods. The dolichoiliac pelvis, so characteristic of the

Triassic coelurosaurians, continued among these dinosaurs through the rest of Mesozoic time and is seen as well in the large Jurassic and Cretaceous carnosaurs.

THE SIGNIFICANCE OF THE TWO TYPES OF TRIASSIC SAURISCHIAN PELVES

The two pelves characteristic of Triassic saurischians show such marked contrasts in form as must indicate, apparently, divergent functional adaptations. The large expansion fore and aft of the ilium, combined with the elongation and narrowing of the pubis and ischium in the dolichoiliac pelvis, indicates changes from a more primitive type in muscle origins, which in turn must have been correlated with certain aspects of locomotion characteristic of the dinosaurs with this pelvic structure.

The forward expansion of the ilium certainly would allow a correlative expansion in this direction of the origins of the ilio-femoralis and ilio-tibialis muscles, which are extensors, while the backward development of the ilium would allow greater room for an expanded ilio-fibularis muscle, a flexor. Also originating on this back portion of the ilium would be other flexors, the flexor tibialis externus and internus. In short, the great expansion of the ilium in the dolichoiliac pelvis would have been correlative with an increase in the large muscles of the hind limb and would imply an increase in strength and effectiveness of these muscles. The remarkable expansion of the extensor muscles that originate on the ilium is of particular significance, as an indication of great power and speed in the recovery phase of the stride.

Romer (1923a) has shown that the change in the position of the femur from an outwardly directed bone in primitive reptiles to a more or less vertically oriented bone in the archosaurian reptiles, and particularly in the saurischian dinosaurs, was accompanied by the transformation of the archosaurian pubis and ischium from the original primitive plate-like form beneath the acetabulum to divergent rod-like bones making a great open space beneath the acetabulum. This, of course, allowed for long and efficient muscles running from the two lower bones of the pelvis to the inwardly pulled femur. In the dolichoiliac type of pelvis we see a progressive advance in this trend of pelvic structure beyond what is characteristic of the brachyiliac pelvis. Thus the greatly elongated pubis and ischium of the pelvis would allow for a long and efficient pubo-ischio-femoralis externus, a flexor, the origins of which were divided by the modification of the pelvis from its primitive form. Other long flexors and extensors attached to these bones would act in concert with the muscles

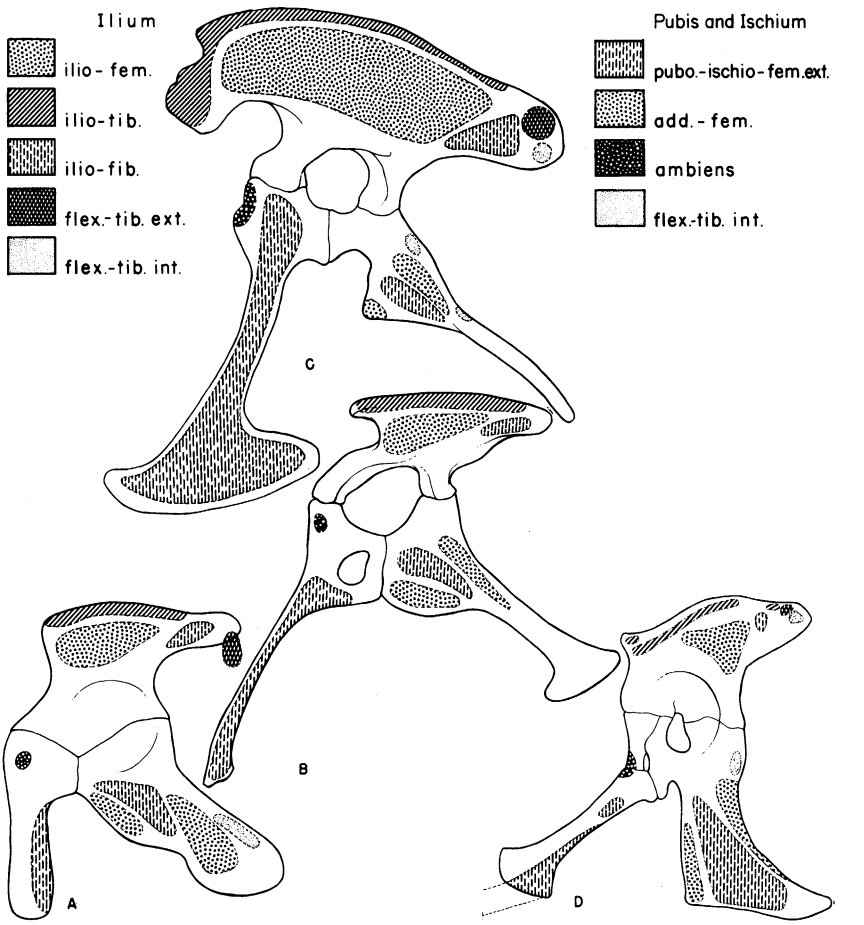

FIG. 3. Origins of muscles on the pelvis, here shown in left lateral view. A. *Erythrosuchus*, a pseudosuchian. B. *Palaeosaurus*, a palaeosaurian saurischian, with the brachyiliac type of pelvis. C. *Tyrannosaurus*, a carnosaurian saurischian, with the dolichoiliac type of pelvis. D. *Alligator*. The origins of the muscles on the brachyiliac type of pelvis probably approached the pattern seen in the pseudosuchians, especially on the ilium, whereas in the dolichoiliac type of pelvis there was a marked expansion of areas for muscle origins. A, C, and D after Romer. *Abbreviations:* add.-fem., adductor femoralis; ambiens, ambiens; flex.-tib. ext., flexor tibialis externus; flex.-tib. int., flexor tibialis internus; ilio-fem., ilio femoralis; ilio-fib., ilio fibularis; ilio-tib., ilio tibialis; pubo.-ischio-fem. ext., pubo-ischio femoralis externus. Not to scale.

that have been here singled out, to insure a powerful and rapid bipedal gait. Particular mention should be made of the fact that a very large proportion of the retraction of the femur in all the saurischians would be applied by the caudofemoralis musculature, which is undoubtedly one reason why the base of the tail was so heavy in these dinosaurs.

It seems probable that the developments of the dolichoiliac saurischian pelvis outlined above were correlated with the perfection of bipedalism. Certainly the increase in size and power of many of the muscles of the hind limbs would be advantageous to a permanently bipedal animal, not only for giving increased thrust to the limbs, but also for affording a quick recovery of each limb after the termination of its thrust. In this connection it should be mentioned that Snyder, who in recent years has made very careful studies of bipedalism in lizards, has shown (1962) that, although the muscles that give power to the hind limbs in these reptiles are very strong, those involved with the recovery of the limb are not significantly different from the same muscles in quadrupedal reptiles. In this connection it is interesting to note that the ilium in these lizards, as in all lizards, is not anteroposteriorly expanded (Snyder, 1962). However, the bipedal lizards, such as *Basiliscus* and *Crotaphytus*, are bipedal only when they are running at a very rapid rate. Their bipedalism is maintained, certainly in part, by their forward speed, so that, when these reptiles are running in the bipedal pose, the tendency of the body to fall forward is not a major factor of locomotion. One might say that theirs is a dynamic bipedalism. In the bipedal dinosaurs, however, bipedalism was both dynamic and static; these reptiles had to maintain the body in a semiupright pose even when they were standing still or walking slowly. Therefore all the muscles of the hind limb would have been very strong, not only those involved with the thrust of the limb but also those that controlled the recovery of the limb—of bringing the limb forward into position under or in front of the center of gravity of the animal. Consequently it is not at all surprising that the permanently bipedal dinosaurs have an elongated ilium, as do birds, and as also do the strongly bipedal saurischians as well as the bipedal ornithischians (which are beyond the purview of the present paper).

If the development of the dolichoiliac pelvis is correlated with bipedalism in the evolution of saurischian dinosaurs, as is here suggested, are there other supporting characters that go with this adaptation? As an answer to this question two such characters may be cited.

In the first place, the sacrum is invariably elongated in the saurischians characterized by the dolichoiliac pelvis. These dinosaurs commonly have five sacral vertebrae and never fewer than four, while dinosaurs with the

TABLE 1
MEASUREMENTS IN MILLIMETERS

	Femur	Tibia and Astragalus	Pes	Humerus	Radius	Manus
Palaeosaurus von Huene, 1932	230	225	220*e*[a]	170	90	148
Thecodontosaurus von Huene, 1932	135	117	148	[80][b]	[53][b]	[56][b]
Plateosaurus von Huene, 1926	680	530	451	400	230	242
Coelophysis (A) A.M.N.H. No. 7223	209	224	247	120	65	95
Coelophysis (B) A.M.N.H. No. 7224	203	221	242	134	82	125
Compsognathus von Huene, 1932, and cast	76	86	100	52	24	45*e*
Ornitholestes A.M.N.H. No. 619; Osborn, 1917[c]	216	171	230	130	87	138
Ornithomimus A.M.N.H. No. 5339; Osborn, 1917	480	540	585	310	230	315
Antrodemus U.S.N.M. No. 4734; Gilmore, 1920	850	743	693	310	222	416
Gorgosaurus N.M.C. No. 2120; Lambe, 1917	1040	1000	1084	324	156	320
Camarasaurus A.M.N.H. No. 5761; Osborn and Mook, 1921	1800	1170	500*e*	1110	790	500

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
N.M.C., National Museum of Canada, Ottawa, Canada
U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D. C.

[a] *e* indicates estimated measurement.
[b] Determined from von Huene's restoration.
[c] Measured from figure.

brachyiliac pelvis always have three sacrals. The advantages of the long sacrum for support is obvious. Therefore it seems probable that the elongated ilia, joined by a long sacrum to which vertebrae from the base of the tail have been added, are indications of reptiles that were habitually

more bipedal than their relatives in which such morphological advances are lacking.

Second, corroborative evidence is furnished by the forelimbs. In those dinosaurs that have the dolichoiliac type of pelvis, the forelimbs were quite obviously not used for locomotion, as is shown either because of their small size or because of the structure of the grasping manus, or both. In

TABLE 2

RATIOS (FEMUR=100) BASED ON MEASUREMENTS GIVEN IN TABLE 1

	Femur	Tibia	Pes	Humerus	Radius	Manus
Palaeosaurus	100	98	96	74	39	64
Thecodontosaurus	100	87	110	59	39	42
Plateosaurus	100	78	70	59	34	36
Coelophysis (A)	100	107	118	57	31	45
Coelophysis (B)	100	109	119	66	40	62
Compsognathus	100	113	132	68	32	59
Ornitholestes	100	79	106	60	40	64
Ornithomimus	100	112	122	65	48	66
Antrodemus	100	87	82	37	26	49
Gorgosaurus	100	96	104	31	15	31
Camarasaurus	100	65	28	61	44	28

the dinosaurs that have the brachyiliac type of pelvis, the forelimbs were evidently capable of being used in part for locomotion; they are either of relatively large size, or the manus is sufficiently broad so that it would have given good support when placed on the ground, or both. These developments, so apparent in the Triassic saurischians, foreshadow the trends of subsequent saurischian evolution.

LIMB PROPORTIONS AND BIPEDALISM

Tables 1 and 2 and the graph that was derived from them (fig. 4) bring out some of the points that are made above concerning the bearing of limb proportions on saurischian relationships. It is readily apparent from the tables that genera characterized by the dolichoiliac pelvis, such as *Coelophysis*, *Compsognathus*, *Ornithomimus*, and *Gorgosaurus*, are typified by a manus much longer than the radius and often equal to the humerus, an indication of the grasping hand with long, flexible fingers that evolved in concert with the development of complete bipedalism, in turn made possible by the advanced form of the pelvis. In *Palaeosaurus*, with a brachyiliac pelvis, the manus is also somewhat longer than the radius, again an

indication of grasping adaptations in a primitive carnivorous dinosaur, but at the same time it is noticeably shorter than the humerus. In *Thecodontosaurus*, *Plateosaurus*, and *Camarasaurus*, a shortening of the hand in relation to both radius and humerus is evident, reaching an extreme in the last-named genus, correlated with the progressive development of secondary quadrupedalism.

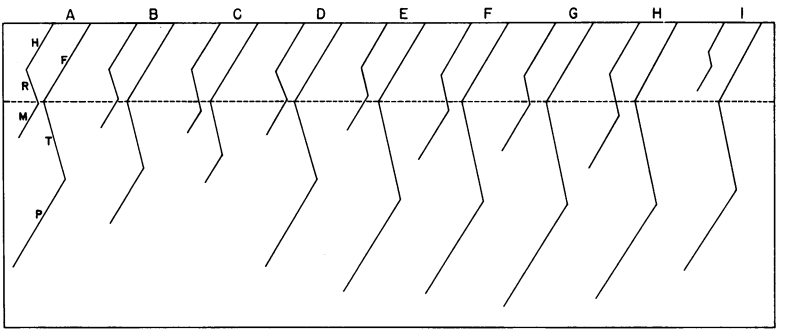

FIG. 4. Graph showing the limb proportions in various saurischians, with the femur as a constant. A. *Thecodontosaurus*. B. *Plateosaurus*. C. *Camarasaurus*. D. *Palaeosaurus*. E. *Coelophysis*, A.M.N.H. No. 7223. F. *Coelophysis*, A.M.N.H. No. 7224. G. *Compsognathus*. H. *Ornithomimus*. I. *Gorgosaurus*. A to D represent dinosaurs with the brachyiliac type of pelvis, and of these *Thecodontosaurus* (A) and *Palaeosaurus* (D) are rather generalized types, with relatively long hind limbs. *Plateosaurus* (B) and *Camarasaurus* (C) illustrate the trend to giantism and quadrupedalism, with a relative reduction in the lower elements of the hind limbs. E to I represent dinosaurs with the dolichoiliac type of pelvis, in which the tibia and pes are long, as an adaptation to bipedalism and rapid running. Note the difference in size of the forelimbs in the two individuals of *Coelophysis* (E, F). *Abbreviations:* F, femur; H, humerus; M, manus; P, pes; R, radius; T, tibia plus astragalus.

It is interesting to note that the two specimens of *Coelophysis* included in figure 4 show considerable differences in the size of the forelimbs. In one the forelimb is less, in the other it is greater, than half of the length of the hind limb. In the latter specimen the hand is very large.

The variability in *Coelophysis* is interesting. The two specimens that show such considerable difference in the size of the forelimbs are preserved together, so there is no doubt that they represent two individuals of a single species. Consequently the differences in their forelimbs, which might indicate a sexual dichotomy so far as this character is concerned, lead one to suspect that, if more complete individuals of other species of dinosaurs were available, similar differences in proportion between fore-

limbs and hind limbs might be apparent among some of them. Therefore some caution should be exercised in basing conclusions on this particular comparison of skeletal characters. Generally speaking, however, the proportion of forelimb to hind limb is a useful criterion in the study of various dinosaurian evolutionary trends, but as is apparent from the case of *Coelophysis*, this evidence cannot be applied within limits that are too narrow.

Let us examine the proportions in the hind limbs. In *Palaeosaurus* the three divisions of the limb are more or less equal in length. In *Thecodontosaurus* the pes is longer than the tibia, and the tibia is shorter than the femur. In *Coelophysis* the extended pes is again longer than the tibia, but the tibia in turn is longer than the femur. Here we see Triassic evidence of two opposed trends among the saurischian dinosaurs. From *Thecodontosaurus* one may follow a trend through *Plateosaurus* to *Camarasaurus* of the Jurassic (although such may not be the actual line of descent in detail), in which the lower parts of the limb become progressively shorter in comparison with the femur, as an adaptation to a graviportal gait. The tibia in *Plateosaurus* is proportionally shorter than that in *Thecodontosaurus*, and the pes is about equal to the tibia in length. The tibia in *Camarasaurus* is proportionately even shorter, and the pes is shorter than the tibia.

In *Coelophysis*, with long lower limb elements, the trend is definitely in the direction of running adaptations, which is continued in later coelurosaurians, for example, in *Compsognathus* of the Jurassic and in *Ornithomimus* of the Cretaceous. In the Jurassic and Cretaceous carnosaurs the tibia is once more shorter than the femur, but this difference is obviously a secondary adaptation to weight. Even in these gigantic bipeds, the pes is bird-like and may be as long as, or longer than, the tibia.

The "carnosaurs" of the Triassic, the palaeosaurs, are revealed as quite independent of the true carnosaurs of Jurassic and Cretaceous age, not only by virtue of their brachyiliac pelvis, but also because of their limb structure, in which the pes is as short as, or shorter than, the tibia and is not adapted to fast running.

Thus it is apparent that complete bipedalism, which was an adaptation for rapid movement across the land and a predatory mode of life, appeared first among the Triassic coelurosaurs. This evolutionary trend was continued within the Jurassic and Cretaceous coelurosaurs, and from it, through a superimposed trend toward giantism, there developed the great line of Jurassic and Cretaceous carnosaurs. It is significant that the evolutionary lines of the coelurosaurs and carnosaurs are those in which the dolichoiliac pelvis is well developed, even from the beginning of their combined history, for this is the structure that would furnish the muscular

base for an efficient bipedalism.

The beginnings of quadrupedalism among the saurischians probably are to be seen among the most primitive prosauropods or plateosaurs, as exemplified by the genus *Thecodontosaurus*. This reptile, even though it was mainly a bipedal type, was probably not so efficient a bipedal animal as its contemporary, *Coelophysis*. It had the brachyiliac pelvis with its limited areas for the origins of various leg muscles that are important for a biped, and it had a short tibia. From this dinosaur as a structural ancestor, it is possible to follow the trend toward giantism and increasing quadrupedalism that is so characteristic of the evolving plateosaurs or prosauropods, and their descendants, the sauropods.

TAXONOMIC CONCLUSIONS

It seems clear that the saurischian dinosaurs of Triassic age can be divided into two groups, one including the more primitive brachyiliac forms in which locomotion was largely bipedal but to some extent quadrupedal, and the other including the dolichoiliac forms in which locomotion was exclusively bipedal. In most previous classifications (see, for example, Romer, 1956), the general practice has been to divide the dolichoiliac forms between the Coelurosauria and the Carnosauria in part, and similarly to divide the brachyiliac forms between the Carnosauria in part, and the Prosauropoda.

It is here maintained that such a classification is unnatural, for it subdivides Triassic genera that are clearly related to one another. Consequently there seems to be much merit in von Huene's clasification of Triassic dinosaurs into the dolichoiliac Coelurosauria and the brachyiliac Pachypodosauria. But if this arrangement is accepted, what becomes of the post-Triassic Carnosauria? An analysis of the Carnosauria as now defined shows that this supposed infraorder, conceived as ranging vertically from the upper part of the Triassic through the remainder of the Mesozoic, is as unnatural a grouping as the horizontal subdivision of brachyiliac saurischians, mentioned above. In short, not all the saurischians presently included within the Carnosauria belong together.

An examination of the Jurassic and Cretaceous carnosaurs, such as *Megalosaurus*, *Antrodemus*, *Gorgosaurus*, *Tyrannosaurus*, and various other related genera, will show that these reptiles, with a dolichoiliac type of pelvis and with small forelimbs, carry the trends of bipedalism established among the Triassic coelurosaurians to extreme culminations. One can hardly imagine a more complete bipedal animal than *Tyrannosaurus*. Therefore it is here maintained that the large carnivorous dinosaurs of

middle and late Mesozoic times are descended from the Triassic coelurosaurians, and that they have nothing to do with the so-called carnosaurs of the Triassic, as is indicated not only by the form of the pelvis and the reduction of the small forelimbs, but also by many other characters such as the construction of the pes, the form of the femur, clearly derived from a coelurosaurian femur with a very distinct and large greater trochanter, the hollowness of the bones, even in the giant forms, and so on.

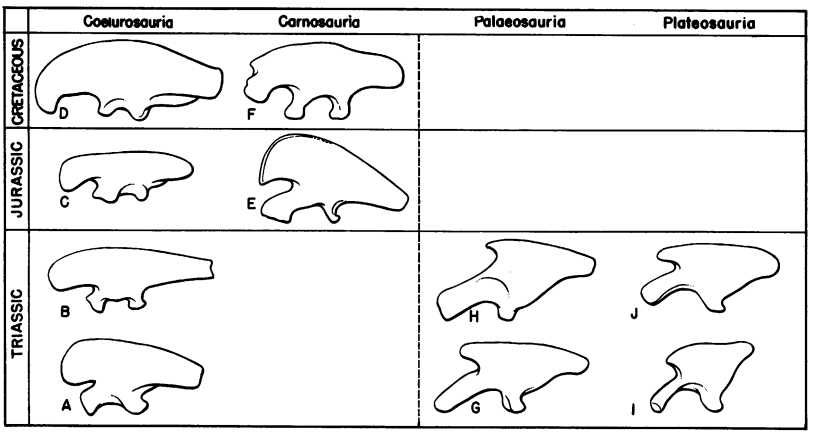

FIG. 5. *Left:* Dolichoiliac ilia of the Coelurosauria and the Carnosauria. *Right:* Brachyiliac ilia of the Palaeosauria and the Plateosauria. A. *Halticosaurus.* B. *Coelophysis.* C. *Ornitholestes.* D. *Ornithomimus.* E. *Antrodemus.* F. *Tyrannosaurus.* G. *Palaeosaurus.* H. *Teratosaurus.* I. *Thecodontosaurus.* J. *Plateosaurus.* The brachyiliac ilium (and pelvis) did not survive beyond the Triassic except as a derived form in the sauropod dinosaurs (not shown). Note the contrasts between the palaeosaurian ilium (G, H), in many previous classifications included among the carnosaurs, and the true carnosaurian ilium (E, F), clearly derived from a coelurosaurian type at or after the close of Triassic time. Modified from von Huene, Osborn, and Gilmore. Not to scale.

It is herein proposed that the name "Carnosauria" be restricted to these large Jurassic and Cretaceous carnivores of coelurosaurian origin, and that the large carnivorous dinosaurs of the Triassic be recognized for what they were, namely, an antecedent and independent adaptation for a predatory mode of life among the brachyiliac group of saurischians. These dinosaurs might very logically be designated as Palaeosauria, to distinguish them from their brachyiliac relatives, the prosauropods or plateosaurs.

If this concept of saurischian relationships is accepted, we may picture an initial origin of the saurischian dinosaurs from thecodont ancestors,

with a very early three-fold radiation in their evolutionary history. The palaeosaurs and the plateosaurs probably diverged from a common stem, one group becoming adapted as small to relatively large carnivores, the other as small to similarly large herbivores. But, in so evolving, these two groups of saurischians retained certain primitive characters, particularly the form of the pelvis inherited from their thecodont ancestors. The third group of Triassic saurischians, the coelurosaurs, apparently evolved quite separately, presumably as a group diverging at a very early date from the primary saurischian stock. These dinosaurs became highly adapted at the very first for bipedalism and rapid movement, as is shown by the structure of the pelvis and the limbs, and the light construction of the skeleton.

During Triassic history the coelurosaurs were small predators, and they remained small (or at the most medium-sized) lightly built predators throughout the remainder of the Mesozoic. From them there arose the carnosaurs at the beginning of the Jurassic, the large predators of middle and late Mesozoic history. The carnosaurs were essentially enlargements of a basic skeletal structure adapted for complete bipedalism and hence for rapid movement, and as such they were very efficient predators on a large scale. The palaeosaurs were, by the nature of their skeletons more "clumsy" than were the carnosaurs, and probably were ill fitted for survival in a changing world. There is no record in the rock sequence that shows any contemporaneous existence of palaeosaurs and carnosaurs, for which reason, among others, it has been supposed that the one group was ancestral to the other. It seems more logical, however, in view of the structural resemblances of the palaeosaurs to the prosauropods and of the carnosaurs to the coelurosaurs, to regard the large Jurassic carnivores as replacements of and not as descendants from the palaeosaurs, as has been argued.

Thus the palaeosaurs, the large carnivorous dinosaurs of the Triassic period, seem to take their place in reptilian history as a brief and sterile experiment in adaptation for predation. They were successful for a time, but, as reptilian life became more complex during the transition from the Triassic to the Jurassic (very significant changes were involved during this crucial aspect of tetrapod evolutionary history), it appears that the palaeosaurs could no longer hold their own, and they disappeared, while their place and their functions in the ecology of those distant times were taken over by the better adapted carnosaurs.

The prosauropods, or plateosaurs, so like the palaeosaurs in some respects, were destined, in contrast to the palaeosaurs, to be the progenitors of a most successful line of saurischian development. Within the prosauropod line the evolutionary trend was in the direction of large size,

quadrupedalism, and a herbivorous diet. Among the late Triassic prosauropods, the plateosaurs and melanorosaurs show this line of evolutionary development to be well advanced. Thus no great step was involved during the Triassic-Jurassic transition that is mentioned, from prosauropod structure to that of the full-fledged sauropod. Giant, quadrupedal, water-loving, herbivorous (and perhaps molluscivorous) sauropods had appeared with the advent of Jurassic history, as had the gigantic carnosaurs, and the interrelationships of these two saurischian groups during middle and late Mesozoic time became one of the characteristic features of life on the land of those days.

This discussion of saurischian relationships may be taxonomically formalized as follows:

Order Saurischia

Archosaurian reptiles with deep skull, well-developed antorbital vacuities and temporal fenestrae, and simple-teeth. Dermal bones have disappeared from shoulder girdle; pelvis basically triradiate, with perforated acetabulum. Anterior limbs in almost all cases smaller than posterior limbs; fourth trochanter of femur never pendent. Pes digitigrade.

Suborder Palaeopoda

Saurischians with primary bipedal adaptations, but partially quadrupedal, forelimbs rather robust and generally adapted in part for locomotion. Bones thick-walled. Pelvis of brachyiliac type, with three sacral vertebrae, relatively short, deep ilium, large acetabulum, long peduncle on ilium for articulation with pubis, with broad, plate-like pubis, usually not expanding distally, and with well-developed obturator foramen. Manus having five digits, outer ones of which may be reduced. Pes comparatively broad, with large, complete pollex directed forward, and fifth digit reduced. Skull relatively small to rather large.

Infraorder Palaeosauria

Small to rather large palaeopods, skull varying from moderate to large size with sharp teeth. Astragalus and calcaneum closely appressed to tibia and fibula.

Families: Ammosauridae; Palaeosauridae; Teratosauridae.

Infraorder Plateosauria (used in place of Prosauropoda, its equivalent, largely for sake of consistency among infraordinal names).

Medium to large palaeopods, with relatively small skull and lanceolate or blade-like teeth. Astragalus and calcaneum distinct tarsal elements.

Families: Thecodontosauridae; Plateosauridae; Melanorosauridae.

Suborder Theropoda

Saurischians with strongly bipedal adaptations, with forelimbs relatively small or slender, not adapted for locomotion. Bones hollow. Pelvis of dolichoiliac type, with four or five sacral vertebrae, elongated ilium, comparatively small acetabulum, and narrow, in many cases rod-like, pubis, distally expanded, lacking obturator foramen. Progressive reduction of digits in manus from lateral to medial side of hand, in most advanced types therefore only two functional fingers. Pes narrow, bird-like, with metatarsal of small

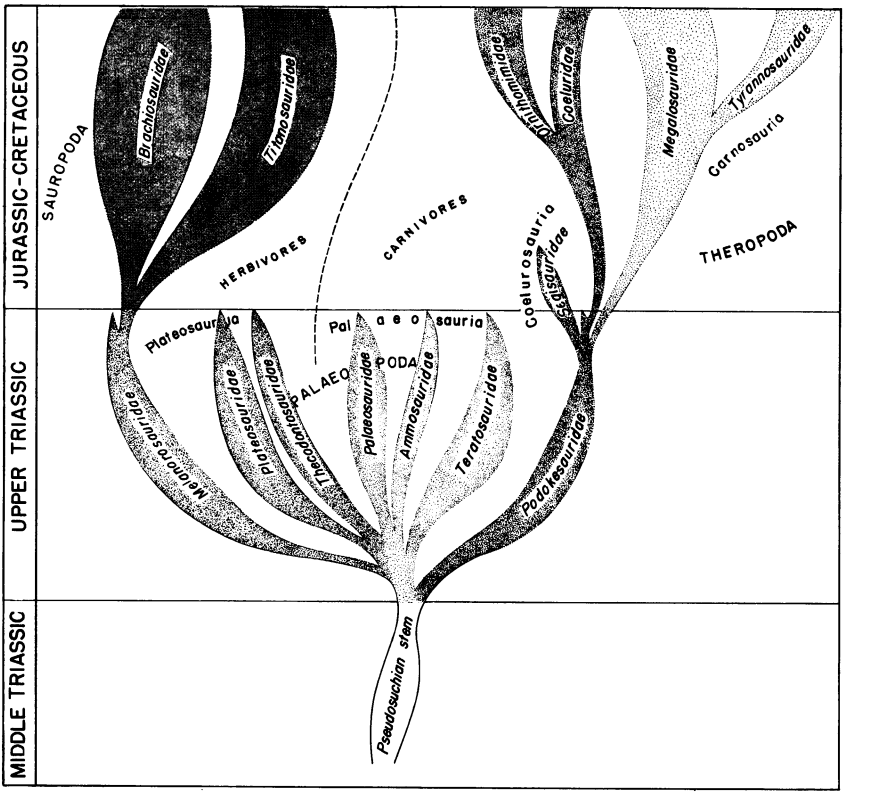

FIG. 6. Suggested phylogenetic relationships of the Saurischia.

pollex incomplete and fifth digit reduced. Skull ranging from being relatively small to extremely large; teeth sharp.

Infraorder Coelurosauria

Small to moderate-sized theropods with thin-walled bones. Skull small, with large, round orbit. Neck of medium length, in longest-necked genera about equal to back in length. Tibia longer than femur. Pes very bird-like, with pollex much reduced, and with astragalus and calcaneum functional parts of tibia and fibula so that there is midtarsal joint.

Families: Podokesauridae; Segisauridae; Coeluridae; Ornithomimidae.

Infraorder Carnosauria

Medium-sized to gigantic theropods, with bones thickened but hollow. Skull large, in most advanced forms extremely large, with vertically elongated orbit. Neck generally much shorter than back. Teeth large and blade-like. End of pubis usually greatly expanded. Tibia shorter than femur. Pes bird-like, with pollex rotated to back, with dorsal process on astragalus, with astragalus and calcaneum forming functional parts of tibia and fibula.

Families: Megalosauridae; Tyrannosauridae.

Suborder Sauropoda

Quadrupedal saurischians, but with forelimbs rarely larger than hind limbs. Gigantic in size, with heavy bones. Pelvis massive, of modified brachyiliac type, with three primary sacral vertebrae, but commonly with addition of caudal to sacral series, with relatively short ilium, large peduncle for pubis, with very large acetabulum and plate-like pubis, not distally expanded, and obturator foramen. Feet short and broad, showing progressive reduction and elimination of ungual phalanges from lateral to medial side of foot. Astragalus and calcaneum large, separate bones. Skull relatively small, with nares commonly shifted backward, lanceolate or peg-like teeth limited to fronts of jaws. Neck exceedingly long, much longer than the back.

Infraorder Cetiosauria

Characters of suborder.

Families: Brachiosauridae; Titanosauridae.

After work on this paper had been started, the author saw two manuscripts that dealt in a general way with the same subject, one by Dr. Alan Charig of the British Museum, the other by Dr. A. W. Crompton and Miss Wapenaar of the South African Museum. Although I am greatly in debt to these colleagues for the privilege of seeing their manuscripts, I wish to state that the work on the present paper was done quite independently of and uninfluenced by the work of Charig and of Crompton and Wapenaar. It will be seen when their papers are published (they may precede the present work) that we have definite differences of opinion concerning various details of saurischian relationships.

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